15. On the Molluscan genus *Cochlitoma* and its Anatomy, with Remarks upon the Variation of two closely-allied Forms. By G. C. Robson, B.A.*

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(Text-figures 1–9.)

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1. Introduction.

In 1914 Mrs. G. B. Longstaff brought from South Africa to England some living examples of the big land-snails usually referred to the genus *Achatina*. A series of observations was planned by herself and the author upon the habits and later development of these forms. These observations were started early in 1915, and, thanks to the satisfactory way in which the animals acclimatized themselves, have been successfully continued and some interesting results obtained which are given elsewhere (*infra*, p. 379). As certain phases of the behaviour of the two forms represented differed rather sharply and as their specific and generic position was uncertain, an examination of their anatomy was undertaken by the author. The principal object of this paper is to provide additional knowledge of the anatomy of the *Achatininæ*; but it also affords an opportunity for discussing how far the individuals of two closely-allied forms agree or differ in all the details of their structure.

The material for this study was presented by Mrs. Longstaff to the Zoological Department of the British Museum (Natural History); and the author is indebted to Mrs. Longstaff, and to Major M. Connolly for information accessory to the study.

The genus *Cochlitoma* was established by Férussac (1821) for a heterogeneous body of forms mostly referable to *Achatina* (s.s.). The name was restricted by Pilsbry (1904) to a small group of the *Achatininæ*. Some thirty-five species were enumerated by Pilsbry, and no substantial modification of the genus has been made since. The group is restricted to S.E. and S. Africa though a few forms straggle up the West Coast, and one species is apparently erroneously recorded from Brazil. Our knowledge of the anatomy consists of a very brief description of the late embryo and embryonic shell, shell-lobes, kidney, jaw, and genitalia of *C. zebra*, due to Semper (1870), a brief description by the same author of *C. granulata* (Krauss), and a short account of some of the internal parts of *C. crawfordi* (Morelet) due to Pilsbry (1904).

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* Communicated by Dr. W. T. Calman, F.Z.S

II. STRUCTURAL.

1. ANATOMY OF *COCHLITOMA ZEBRA* (Brug.) var. *OBESA*.

Two specimens were available for dissection, both almost fully grown and referable to Pfeiffer's variety *obesa*. They measure 83 × 47 mm. and 82 × 47 mm. respectively, and are thus a little shorter than Pfeiffer's type (1854). In the following description the two examples are referred to as z_1 and z_2 respectively.

External Features.

(1) *Shell.*—The conchological status and synonymy has been discussed by Pilsbry (1904). It is necessary, however, to refer in some detail to these features in order to show what relation there is between the variation of external and internal characters.

In Pilsbry's description the *columella* is "arcuate." In z_1 it is perfectly straight and contrasts strikingly with the arcuate form seen in z_2. In z_1 there is a well-marked callus which is absent in z_2. The coloration, invariably regarded as an inconstant feature, is markedly different in the two forms. Z_2 agrees with Pilsbry's description, but in z_1 the dark stripes are often twice and thrice the size of the white ones. Both examples have $7\frac{1}{8}$ whorls. The aperture varies. In z_1 it is wider and shorter than that of z_2, measuring 48 × 27·5 mm. as compared with 50·5 × 26 mm.

The sculpture is, as Pilsbry says, granoso-decussate. But in both forms the spiral striæ are weak, so that, as a result, the transverse ribbing is more marked than in the variety *fulgurata*. In z_2 the spiral striation is stronger than in z_1. This *sculpture* starts at about half-way round the second whorl in z_1 and three quarters of the way round the second whorl in z_2. It is continued in both cases to the end of the sixth whorl. A peculiar character seen in the var. *fulgurata* as well, viz. the enlargement of some of the longitudinal bands of granules, is seen in a weak condition in z_1, but is absent in z_2. There is, however, in the same position an abrupt enlargement of all the granules.

(2) *Coloration.*—This is more fully dealt with in Mrs. Longstaff's paper.

(3) *Mantle-folds, etc.*—The cervical lobe was thick, narrow, and pointed in z_1. That of z_2 differed only in being much longer. The posterior lobe is irregular in shape and has two main surfaces, one vertical (between which and the cervical lobe the anal canal runs) and one horizontal. The latter is continuous with the shell-lobe.

(4) *Anus, etc.*—The *anus* and *pneumostome* lie more or less closely together. The latter is interior to and rather below the

former. The *ureter* opens by a wide and non-plicate aperture anteriorly to the anus. In front of the ureter lies a small lobe. A certain amount of distortion made it impossible to compare z_1 and z_2 in this respect.

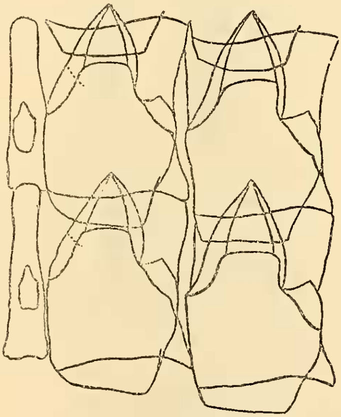
Internal Anatomy.

(1) *Alimentary Canal.*

The jaw was examined only in the case of z_2, that of z_1 being previously damaged.

Viewed anteriorly the *jaw* is markedly lunate and its antero-dorsal surface is very wide. The interior surface is covered by a fairly dense cuticle which is continued backwards and round the sides and bottom of the mouth. It is more dense dorsally and is continued posteriorly for about 5–6 mm., but is not continued on to the antero-dorsal plate. There is on this cuticle a faint but definite striation. The weak ribbing seen in var. *fulgurata* is represented only by a few irregular faint dark lines which can be seen under a high power.

Text-figure 1.



Cochlitoma zebra var. *obesa*.

Radula; median and admedian teeth. Position of degenerate entocone shown by dotted line.

The *radula*. (Text-fig. 1.)

Formula:—	z_1	80.	1.	80.	×133.	
	z_2	69.	1.	69.	×133.	
Another example from the Gwatkin collection		67.	1.	67.	×124.	±1.

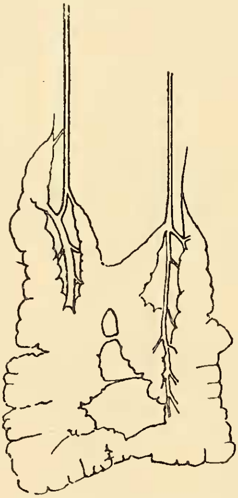
These figures represent maxima.

For the purpose of this study only the median, the first two admedian and the adlateral teeth were compared.

All the specimens examined showed a slender median tooth with simple, rather piriform cusp. In z_2 this is abnormal and irregularly bicuspid. The admedian teeth have large heavily conical mesocones, rather weak ectocones, and degenerate entocones. In z_2 the latter were very meagrely developed. The base of the mesocones is very heavy, broad, and deep. Its inferior edge is usually, but not always, turned upwards and outwards. The adlaterals (e. g., about the fortieth) are bicuspid with low stout mesocones and a very deep narrow basal plate.

The *pharynx*.—The attachment of the pharyngeal muscles is semilunar in shape. It will be more fully discussed under var. *fulgurata*. There is an exceptionally short œsophagus passing into a *crop* measuring approximately 20 mm. ±3. Interiorly the latter exhibits a number of longitudinal folds with transverse secondary connecting ridges, which form a rough trabecular system. In both examples the crop is covered by the salivary glands. The ducts of the latter originate in the usual position. The glands themselves are in both cases asymmetrical, the left being larger than the right. They are joined together in the median line by two organic connections, one anterior, the other posterior. Pilsbry (1919) mentions that the glands of *Achatina schweinfurthii* von Marts. are similarly joined, but only anteriorly. Between z_1 and z_2 are several considerable differences in detail.

Text-figure 2.



Cochlitoma zebra var. *obesa*.

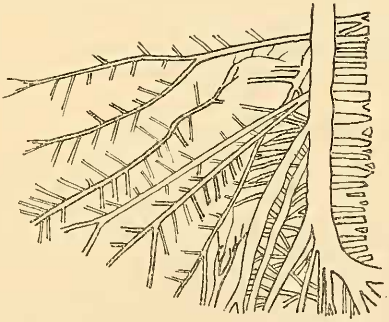
Salivary glands.

The crop is succeeded by a narrow continuation of the œsophagus which fairly rapidly widens into the anterior part of the *stomach*, which is thin-walled and crescentic. At the base of the third whorl this gives off a large reniform, muscular sac which may provisionally be regarded as the representative of the cæcum found in many Prosobranchs, Opisthobranchs, and certain Basommatophora. This structure has been noticed by Wiegmann (1898) in *Achatina panthera*. It is not present in all Stylommatophora, but occurs in *Bulimus* (*Borus*) *ovatus* and *proximus* according to Plate (1896). Owing to the fact that the anterior part of the stomach opens close to the pylorus of the intestine, we may fairly assume that the large muscular part does represent the originally smaller cæcum. The muscular portion receives the posterior hepatic duct and is very thick-walled, its inner surface being furnished with characteristic ridges. A more detailed description of these organs is given under var. *fulgurata*.

(2) *Circulatory* and *Respiratory System*.

As both animals had been dead for some time previous to dissection, it was impossible to make an injection of the circulatory system. This is all the more to be regretted as some interesting results might be expected from the study of the elaborate cerebral vascular system noticed when dissecting the circumœsophageal nerve complex. The *pericardium* is under one-third the size of the kidney, a smaller proportion than usual. The *auricle*, as usual, is thin-walled and is attached to the adrenal wall of the pericardium for about one-third of its length. It is irregular in shape, but presents a broad end to the *ventricle*. The latter is of a narrow, ovoid shape and is slightly shorter

Text-figure 3.



Cochlitoma zebra var. *obesa*.
Anterior end of pulmonary vein.

than the auricle. Paired auriculo-ventricular valves of a simple nature were found; but apparently there is no aortic valve. The course of the *aorta* was not followed, but its anterior branch was found passing into the pharynx in the usual position; before doing which, it gives off several branches which contribute to the cerebral vascular system referred to above. The *pulmonary vein* (text-fig. 3) is very large. On its left-hand side and particularly towards the anterior end of the pulmonary cavity, it sends out several large branches which become very much concentrated anteriorly. On the left-hand side there were no particularly large vessels. In z_1 the pulmonary vein lies close to the ureter—on an average 5 mm. from it. In the last respect z_2 differed from z_1, being much further away from the ureter. The latter condition is seen in *Archachatina bicarinata* (Deshayes (1821)) and also apparently in *Limicolaria*. The anterior concentration of large secondary vessels is seen in *Achatina chrysoleuca* (Pilsbry (1904)) and in *Arch. bicarinata*.

(3) *Renal System.*

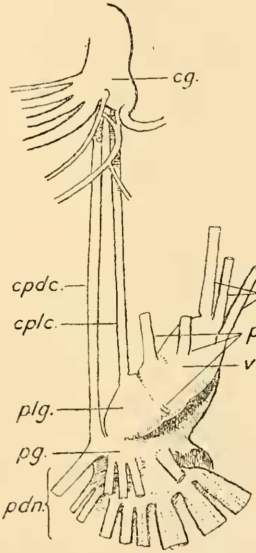
The kidney measures 58 × 11–12 mm. in z_1 and 42 × 9–10 mm. in z_2. Anteriorly it narrows off slightly to an obtuse point. Posteriorly it exhibits a curious diagonal groove on its under surface which separates off a sort of posterior lobe. This occurs in both z_1 and z_2; but it is doubtful whether it is of systematic value, though it was absent from both specimens of var. *fulgurata*. Another interesting feature is the presence of a sort of "heel" projecting from the posterior end of the kidney. In both forms this was disposed in prolongation of the main axis of the organ.

(4) *Nervous System.* (Text-fig. 4.)

General.—In the adult the central nervous system is covered over by a dense layer of connective tissue which involves the main ganglia and roots. This layer, which has been commented upon by previous authors (Nabias (1894)), is exceedingly difficult to dissect away even in young forms, while in most adults it appears to have complete histological union with the surface of the ganglia. In young forms it is less extensively developed, less closely applied to the ganglia and more hyaline. The growth of this sheath involves the anterior aorta and its cerebral branches. It is hoped that a future work may be devoted to the study of this sheath. This much may, however, be stated that, whatever functions it may or may not have acquired in the course of its intimate association with the surface layer of the ganglia, it has certainly developed a great importance as providing additional holdfasts for the muscles of the head and anterior part of the body. For example, the rhinophorial retractors appear to be partly dependent on the postero-lateral extension of this sheath. Interesting analogies are suggested by this structure, particularly on the subject of its function as a protection for the brain and support for muscles, but they must be deferred to a later date.

The cerebral ganglia are joined by a stout commissure. The several elements of the visceral commissure are very closely united, and on the right side no distinction between abdominal and visceral ganglia could be made out. On the left, the line of demarcation between the visceral and pallial ganglia was fairly plain, that between the visceral and abdominal less plain. There are no pallio-pedal connectives, the centres being closely approximated. The pedal centres are likewise intimately fused to form a single mass, all that indicates an originally separate condition being a faint median ventral furrow. The right side of this complex is larger than the left.

Text-figure 4.



Cochlitoma zebra var. *obesa.*

Central nervous system (left moiety).

cpdc. = cerebro-pedal connective. *cplc.* = cerebro-pleural connective. *cg.* = cerebral ganglion. *pg-* = pedal ganglion. *plg.* = pleural ganglion. *vag.* = viscero-abdominal ganglion. *vn.*=visceral nerves. *pln.*=pallial nerves. *pdn.*=pedal nerves.

Pedal Nerves.—In counting the number of nerve-roots arising from all ganglia, allowance has to be made for a certain amount of error due to the density of the sheath and the consequent impossibility of being certain that adjacent roots are separate. In z_1 there are eighteen pedal roots on the left and sixteen (three fused) on the right. In both specimens a grouping of the pedal nerves into two tiers, one above the other, could be made out. The upper tier consists of five roots, one anterior three median (usually fused) and one posterior. Certain of the lower tier roots are separate in origin but enclosed together for the first 2–3 mm. of their length in common sheaths of connective tissue. The arrangement of these differs from side to side and in individuals. In z_2 there were seventeen roots on each side.

Pallial and Visceral Nerves.—In neither example can it be asserted that any nerve arises from the pallial centres. The latter (as defined by the position of the cerebral-pallial connective) is clearly marked off posteriorly from its neighbour and no pallial root arises from it on either side. Pallial nerves arise, however, from the posterior ganglion mass (viscero-abdominal). We can only conclude that fusion of ganglia has gone so far that the slight external divisions are not reflected internally. On the right there is only one pallial nerve, on the left three. There are three main abdominal and visceral nerves arising from the posterior end of the complex. Z_1 and z_2 agree in these particulars.

Cerebral Nerves.—From the cerebral ganglia there arise on each side nine roots in z_1, eight in z_2. These consist of three large labial and pharyngeal nerves, two rhinophorial, optic, buccal connectives, and two (one in z_2) of uncertain distribution. There is a certain amount of unimportant difference in the position and distribution of the nerves between z_1 and z_2. The buccal commissure is symmetrical and the ganglia closely fused. On each side six pharyngeal nerves originate from these ganglia, the origin of which is asymmetrical.

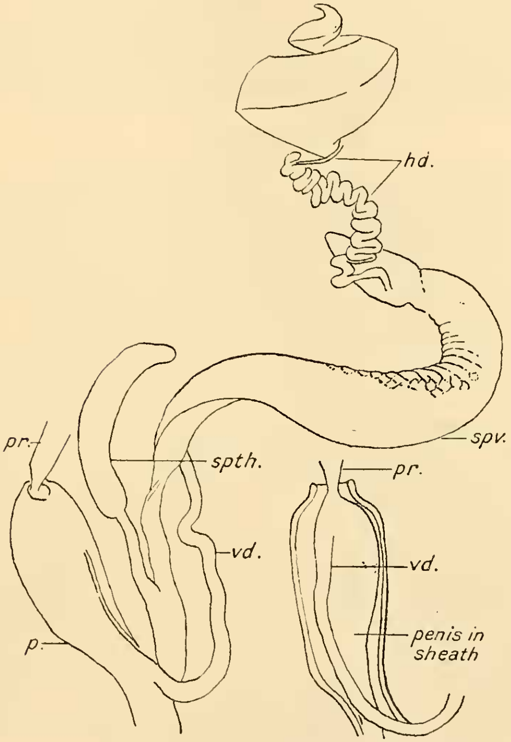
The optic nerve is exceedingly slender and arises a little posterior to the rhinophorial nerve. It enters the sheath of the rhinophore above the latter nerve. In z_2 the base of the rhinophore is innervated by a separate nerve arising just anteriorly to the first mentioned rhinophorial nerve. Amaudrut (1886) refers the innervation of the base of the rhinophores in *Achatina panthera* to a nerve arising from the anterior lobe. There is in *C. zebra* no distinction into three distinct lobes as Amaudrut described for his species, though traces of a fairly distinct lobe corresponding to Amaudrut's "lobe de sensibilité" could be seen in z_2. Again, there is no fine branch of the rhinophorial nerve as there is in *A. panthera.*

(5) *Reproductive System.*

Neither specimen dissected was apparently in a state of reproductive activity. The gonad which is situated in the 2–3 whorl, is succeeded by a slender duct which is straight for about 6 mm. and then becomes stouter and more convoluted. In the third whorl this passes into the *spermoviduct.* The male portion of this, as in the Helicidæ, forms a sort of gutter incompletely covered by two more or less overlapping ridges. The ducts of the numerous prostatic follicles open into the bottom of this. The *prostate* invests one side of the spermoviduct over practically its whole length and projects into the lumen of the uterus. The upper end of the latter is much folded, the lower end smooth.

The *vagina* is short (22 mm. in both cases) as compared with the long spermoviduct. The *spermatheca* has a characteristic duct with a broad and stout basal portion narrowing to a short thin section which expands to the long, truncheon-shaped spermatheca. The duct measures 17 mm. in z_1 and is longer in z_2. The latter appears not to have attained its full development, so that the spermatheca may grow at the expense of the duct. The common duct of vagina and spermatheca measures 15·5 mm. in z_2 and only 8 mm. in z_1.

Text-figure 5.



Cochlitoma zebra var. *obesa*.

Genitalia. For lettering see text-fig. 9, p. 262.

The *vas deferens* measures 52 mm. in z_2 and 37 mm. in z_1. It passes to the base of the penis and is inserted into the latter at a point about two-thirds of the way from its apex downwards. In z_2 the point of insertion is lower down. The penis sheath is *complete*, and the retractor is a branch of the right ocular band.

In the internal structure of the penis there is a marked difference between the two forms. In z_1 the penis fits closely into its sheath. In z_2 the neck of the sheath through which the retractor passes is very much thickened and the retractor passed down it some way before it meets the penis, which is thus shorter than in z_1.

2. COCHLITOMA ZEBRA var. FULGURATA (Pfeiffer).

Two specimens were dissected, measuring 115 mm. and 94 mm. These are designated f_1 and f_2 respectively.

External Features.

(1) *Shell.*—The aperture is in both cases more effuse ventrally than in the typical form, and the columella is sinuous in both cases. The sculpture starts in f_1 on whorl $1\frac{1}{2}$–$1\frac{3}{4}$, in f_2 on whorl $1\frac{3}{4}$–2. The character of the sculpture was mainly based upon f_2 as f_1 was very much worn. It consists of flattish blister-like decussations of a more delicate texture and quality than in *zebra.* As in var. *obesa* they are crowded at the upper sutures. There is a band formed of enlarged granules running spirally round the upper whorls. In f_2 this is lower down on each whorl than in f_1. There are eight whorls in each case, and the granules extend as 3–5 sutural rows on to the last but one whorl in f_1. In f_2 these are only very slightly represented, though the shell is less worn. The character of the colour banding varies a good deal between the two specimens, but it is substantially different from var. *obesa.*

(2) *Coloration.*—A detailed account of this feature will be found in Mrs. Longstaff's paper.

(3) *Mantle-folds, etc.*—The cervical lobe is broad and flat in f_1, narrow and pointed in f_2. The posterior lobes are not different from those of var. *obesa.*

The *anus* and *pneumostome* lie very much as they do in var. *obesa* and their general character is the same. A special lobe is found parallel to and below the cervical lobe which more or less screens the urinary aperture as in var. *obesa.*

Internal Anatomy.

(1) *Alimentary Canal.*

The *jaws* agree in both cases. They are flatly lunate when viewed anteriorly. The upper surface is of the same average width all the way round and is rather narrow in proportion to its width. There are faint and irregular signs of broad ribbing and traces of faint striation.

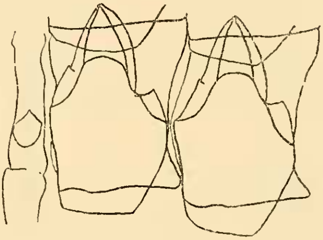
The jaw is at once distinguished from that of var. *obesa* by its narrowness and the parallel edges of its upper plate.

The *radula* (text-fig. 6) has the formula:—

f_1 .... 71. 1. 71. ×143.
f_2 .... 78. 1. 78. ×123.

The median tooth is short-cusped and much wider than that of var. *obesa.* The first admedian has a stout but rather low mesocone, a fairly well-developed ectocone, and only the faintest trace of an entocone. It is probable, though not quite certain, that it is less well-developed than in var. *obesa.* The basal plate is uniformly less deep than in the latter, broader and more rectangular. Very little difference can be noticed in the adlaterals. A curious abnormality was to be observed in f_1. Commencing at the sixteenth transverse row, a short series of about three rows of teeth is dwarfed and crowded closely together.

Text-figure 6.



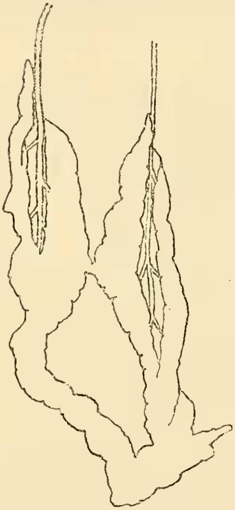
Cochlitoma zebra var. *fulgurata.*
Radula; median and admedian teeth.

The *pharynx.*—Four main pharyngeal retractors pass through the subcerebral orifice and spread out in a broad fan-shaped fascia which, as in var. *obesa*, has a semi-lunar insertion on the postero-ventral surface of the pharynx. There is a short œsophagus which passes insensibly into the crop. Internally a greater complication of the internal longitudinal folds, a greater frequency of transverse ridges, and a greater general thickness enables us to assume that the crop starts about 10 mm. from the pharynx. Measured from this point the crops of f_1 and f_2 are 39 ± 3 and 26 ± 3 mm. in length respectively.

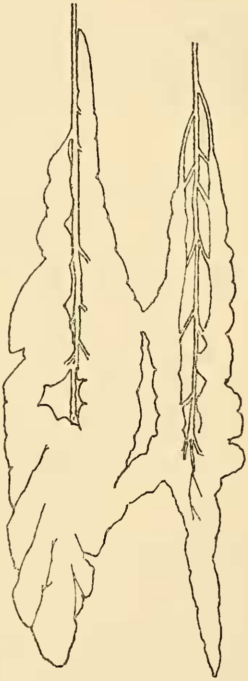
The *salivary glands* (text-figs. 7 & 8) differ extensively in f_1 and f_2. In general they correspond to those described above. The crop passes into the anterior part of the *stomach*, in f_1 abruptly, in f_2 gradually. The *stomach* exhibits considerable differences in f_1 and f_2. Thus in f_1 the shape is piriform and in f_2 irregular. But there is no character which differentiates these forms from var. *obesa.*

The relation between the anterior and posterior parts of the stomach (or stomach and cæcum) has not been commented upon at any length save in a general way by Wiegmann (1898). The stomach as a whole is bent on itself, and the apex of the bend is principally occupied by the muscular portion. The floor of the latter shows a distinct ridge which separates the entrance of the fore gut from the intestinal pylorus. The longitudinal muscular folds of the stomach cross this ridge at right angles. In both forms (and in *obesa* as well) the folds begin abruptly on the anterior side of the ridge, cross it and pass down the intestine for a short way. Very characteristic is a strongly developed ridge commencing close to the posterior hepatic orifice and running straight down the proximal part of the intestine. Possibly an incomplete or degenerate *typhlosole*, it begins as a thick pillar and gradually diminishes in size. On one side it is bent on itself and accompanied by a smaller narrow ridge, which is separated from it by a narrow space. This space is continued up to the posterior hepatic orifice and round the well-marked angle between the ridge on the floor of the muscular portion and its anterior wall. It passes over on to the anterior side of the ridge and communicates with the anterior hepatic orifice.

Text-figure 7.



Text-figure 8.



Text-fig. 7.—*Cochlitoma zebra* var. *fulgurata.* Salivary glands (f_2) (semi-diagrammatic).

Text-fig. 8.—*Cochlitoma zebra* var. *fulgurata.* Salivary glands (f_1) (semi-diagrammatic).

In these general features there was no difference between the two varieties or the examples of each.

Neither *intestine* nor *anus* differs from those of var. *obesa.*

(2) *Circulatory* and *Respiratory System.*

The pericardium is slightly less than half the size of the kidney. In both cases the ventricle is broader and shorter than in *zebra.* The pulmonary vein of f_1 was affected by disease. That of f_2 had its secondary branches more evenly distributed than z_1 and z_2. As in z_2 the pulmonary vein was a considerable distance from the ureter.

(3) *Renal System.*

The kidney measured:—

f_1 .... $55 \pm 3 \times 13$ mm.
f_2 .... $36 \pm 2 \times 14$ mm.

Even with this variation the kidney is in general appearance broader than that of var. *obesa.* There is no posterior groove and the posterior appendage tends to lie *at right angles* to the main axis of the kidney.

(4) *Nervous System.*

The remarks made above (p. 254) about the connective tissue sheath and its general significance are relevant in the case of this variety.

Cerebral Ganglia.—The general shape resembles those of var. *obesa.* The position and origin of the main roots are more or less identical though there are differences of detail. The buccal ganglia are fairly closely approximated in f_2, but *widely separated by a distinctly differentiated commissure in* f_1. Each buccal ganglion gives off four antero-lateral and one posterior nerve. As in *zebra*, there are three large labial and pharyngeal nerves. The innermost supplies the lower lip, the next innervates the sides of the mouth and sends a branch to the anterior tentacle (a branch found in *obesa*), while the third gives off lateral and superior labial and a mandibular branch. Behind and above there arises a very slender auditory nerve and behind and above this the rhinophorial nerve.

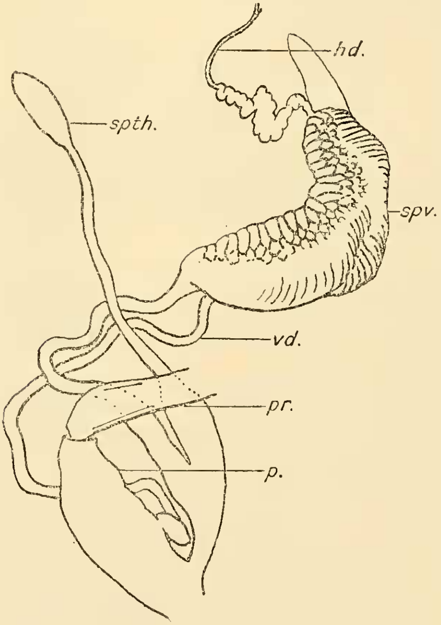
Between this variety and *obesa* the most important differences appear to be the greater apparent differentiation of the "lobule de sensibilité" and the fact that there are only seven nerves aside in this variety.

Pedal Ganglia, etc.—The cerebro-pedal connectives are long and slender. As in var. *obesa* they enter the pedal ganglia in an antero-dorsal position. There is the same tiered arrangement of the pedal nerves, and in f_2 there are seventeen roots aside and probably the same number in f_1.

There was not nearly so much enclosure of adjacent pedal roots in common sheaths as in var. *obesa.*

Pallial Ganglia, etc.—The cerebro-pallial connectives join the pallial ganglia in exactly the same position in the two varieties, and in this area the arrangement is very similar to that of var. *obesa.* There appears to be no visible distinction between the pallial, visceral, and abdominal ganglia. There is the same asymmetry with regard to the pallial roots, there being three on the left and only one on the right. This asymmetry was observed by Amaudrut in *A. panthera* (1886). The three main abdominal nerves came off a common root in f_2.

Text-figure 9.



Cochlitoma zebra var. *fulgurata.*

Genitalia.

hd. = hermaphrodite duct. *spv.* = spermoviduct. *spth.* = spermatheca.
vd. = vas deferens. *pr.* = penis retractor. *p.* = penis.

(5) *Reproductive System.*

The gonad lies between the second and third whorls. The *hermaphrodite duct*, *spermoviduct*, and *albumen gland* show no difference from those of *obesa.* The *vagina* is long, measuring 27 in f_2 and 34 mm. in f_1. The spermatheca is spatulate in both examples and the duct is long (38 ± 2 in f_1 and 35 ± 2 mm. in f_2). The vas deferens measures 56 ± 2 mm. in f_1 and 41 ± 2 mm. in f_2, and therefore may be regarded as long, though the anomalous condition seen in var. *obesa* shows that this is not a character to be relied upon. It enters the penis sheath in f_2 half-way down its length. In f_1 its point of insertion is doubtful. With regard to the actual junction of the vas deferens and penis a general approximation is made in f_2 to the condition seen in z_2. The length of the vagina and the form and proportions of the spermatheca differentiate both examples dissected from var. *obesa*.

III. GENETIC AFFINITIES AND VARIATION OF *COCHLITOMA ZEBRA* VAR. *OBESA* AND *FULGURATA*.

The author does not feel justified in altering the position assigned by Connolly (1912) and others to *C. fulgurata* Pfr. as a variety of *C. zebra*. Although it differs from var. *obesa* in certain conchological and anatomical features, conchological intermediates (British Museum, Zool. Dept.) have been found which cannot be disregarded.

It is a commonplace among systematists that between two varieties of a "species" or two "closely allied species" there may be complete agreement in certain respects and difference in others. It is plain, however, that in the case of the two varieties of *C. zebra*, the *individuals* of a variety do not differ from those of a closely allied variety in respect of the *same* characters. Though they may all differ to the same extent from the typical form in respect of, for example, two characters, they do not all show the same degree of difference in their other characters. In the present instance var. *obesa* differs from var. *fulgurata* in having a truncheon-shaped spermatheca with a short duct as opposed to a spatulate spermatheca with a long duct, and a shell with narrow brown and white stripes as opposed to broad and jagged stripes of brown and yellow. But one individual of *fulgurata* agreed with *obesa* in having a narrow and pointed cervical lobe, while the other *obesa* had a broad flat one. Of the three forms that agreed in this respect one (z_1) differed from the two *fulgurata* and z_2 in having a straight columella as opposed to a sinuous one. Again, one example of *fulgurata* and one of *obesa* agreed approximately in the length of the vas deferens, while one *fulgurata* agreed with the two *obesa* in the relation of kidney to pericardium and differed from its fellow. Again, the same *obesa* agreed with *fulgurata* (*cf.* above) in respect of the columella, and yet the relationships of the two *obesa* are reversed in respect of the form of the rhachidian tooth of the radula. Two conclusions may be drawn from the above data:—

(1) That the amount of correlated variation in this case is very slight.

(2) That the degree of difference or agreement is independent of the type of organ or structure involved; though glandular tissues appear to be more unstable than the others.

The size and possibly the shape of glands, however, are probably conditioned by the amount of secretion which is usually subject to periodic variation.

The late B. F. Cummings and the present author put forward a suggestion ("X" 1914) that internal structures would probably turn out to be better guides for ordinal and generic characters, while the external structures register specific and varietal differences more readily. There would now be grounds for considering that the internal anatomy is neither more nor less variable than the external structures.

The small amount of correlated variation in these forms, and the irregular fashion in which individuals of a variety agree or differ from those of a closely allied variety, make it very difficult to distinguish the "species" and "varieties" of current taxonomy in this case. The author has come to the same conclusion as Pilsbry (1912), that "a philosophic method of dealing with intraspecific differentiation is one of the greatest needs of systematic zoology." "Species" and "variety" appear to the author, and also apparently to Dr. Pilsbry, to be an association of forms which in their mutual relationship may be singularly unstable and loosely associated. It is not merely a question of the extreme linear or graduated variability with which all naturalists are familiar. In that case species and varieties are equivalent for example to the divisions of time into hours and minutes as convenient, if arbitrary, units. In the present case, however, the large amount of uncorrelated variation between *individuals* of a "variety" leaves a very strong suspicion in the mind that along with linear (or graduated) variability there may exist a radial * tendency of association which cannot be expressed in arbitrary subdivisions. If this impression is substantiated by other evidence it will remain to discover which of the two tendencies corresponds more closely with the results of cytology and genetics. The author is indebted to Professor Duerden for permission to state that certain conclusions arrived at by him in the course of work upon the Ostrich are in line with the facts recorded above.

IV. ON THE CLASSIFICATION OF THE *ACHATININÆ* AND THE POSITION OF THE GENUS *COCHLITOMA*.

Pilsbry (1904) has taken the shell as his basis for arranging the twelve genera of Achatininæ, and his first subdivision into two main groups depends upon the presence or absence of sculpture on the embryonic whorls. We cannot, however, disregard the fact that examination of a number of examples in the British Museum collection has made it clear that the sculpture of the embryonic whorls of these forms differs in individuals of the same species. Thus, in two examples of *Burtoa nilotica* the commencement of the sculpture varied from whorl $2\frac{1}{4}$ to whorl $3\frac{1}{4}$. The result of this is that it is possible to find examples of species placed by Pilsbry in his first group ("embryonic whorls sculptured") with sculpture starting in exactly the same spot as it does in species placed in the second group. For example, in the two examples of *C. zebra* var. *fulgurata* in the British Museum the sculpture starts on whorl $2\frac{1}{4}$, the same position as in an otherwise typical *Burtoa nilotica*. A more serious consequence is that Pilsbry's arrangement cuts right across several other potential arrangements of equal and possibly greater importance. The character of the penis retractor which is either inserted on the diaphragm or on the right ocular bend, that of the penis ring-muscle, whether a complete sheath or annular, and the character of the admedian teeth, whether having three, two, or one cusps, are three out of many characters which might be used as a basis and, if used, would give a different arrangement of the genera and species.

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* The antithesis between *linear* and *radial* variation used in this connection may be criticized as vague. It is difficult, however, to find two terms which express adequately the fact that an individual of a "species" placed in a series presumed to express descent may, however, exhibit characters which qualify it for a place in another series not necessarily expressing the same line of descent.

If a classification based upon the *shell* gives (as it certainly does) a different result from that based upon the radular characters, and if the latter yields a different scheme from that based upon the insertion of the penis retractor, it is plain that any classification based upon a single character must be arbitrary*. What is required is a complete knowledge of the variation and mode of inheritance of all the important structures in each genus and a classification based upon the greatest measure of agreement among the various forms.

The anatomy of all the genera and species of this subfamily is not known. It may be, therefore, argued that a provisional arrangement based upon the only organ known in the species, viz. the shell, is justified.

If, however, the object of classification is a correct arrangement expressed in terms of relationship, it would seem best, in cases such as the present, to select from all the available data a combination of the more important characters as a basis and to arrange the species upon it as far as possible, even if some are left vaguely designated as "Achatina." The selection of a character (in this case the shell) that will enable *every* species, whether known completely or not, to be given a definite place, involves the production of a scheme that sooner or later has to be revised, if not abandoned altogether.

With regard to the conchological genus *Cochlitoma* itself, only three species are known anatomically, and of these only the two varieties of *zebra* are known in any detail. But it is very doubtful whether these four forms are referable to the same genus. *C. crawfordi* differs from the others in the remarkable insertion of its penis retractor. *C. granulata* does not fall into line in the character of its penis sheath. These two forms also appear to be separate from the other forms in respect of the jaw (*v. supra*). Conchologically some of the forms included are indistinguishable from *Achatina* (s.s.). We therefore conclude that the present conception of the genus *Cochlitoma* is unsound. Fresh data are, however, necessary before a final arrangement of the forms involved can be made.

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* *Note.*—It is conceivable that intensive study may show that, within a given genus, one organ or structure reflects genetic modifications better than others. But this has yet to be proved.

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